第25卷 第4期
1987年10月

古 脊 椎 动 物 学 报
VERTEBRATA PALASIATICA

pp. 283—296
figs. 1—2, pl. I—II

江苏泗洪下草湾中中新世脊椎动物群
——7. 山河狸科(哺乳纲,啮齿目)

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关键词 江苏 中新世 下草湾组 山河狸科

内 容 提 要

以前作为 *Prosciurus* sp. 报道的下草湾动物群的山河狸,被订正为 *Ansomys orientalis* gen. et sp. nov.。山东晚渐新世的 *Prosciurus*? *shantungensis* Rensberger et Li, 1986 被纳入该新属。它们和欧洲早中新世的 *Plesispermophilus*? *descedens* Dehm, 1950 一起被归入一新的亚科——Ansomyinae。本文还探讨了山河狸各亚科的系统发育关系。

山河狸化石不很常见,在我国的发现更为零星。本文记述的材料,系近年于江苏泗洪县双沟、松林庄及郑集三处的下草湾组采集的。前两地点的化石,已作为 *Prosciurus* sp. 报道(李传夔等,1983)。但材料的进一步观察表明,这些牙齿的形态和构造与 *Prosciurus* 属的相差很大,应代表山河狸科一新的属、种。新属的特征与迄今所限定的山河狸各亚科的定义也不符,故在此予以报道。

文中使用的牙齿构造术语,引自伦斯博格(Rensberger, 1981, 1983, 1986)对山河狸的描述,其译名主要采用王伴月(1986)所拟。

承邱占祥等同志阅读及修改文稿,E. 林赛教授修改英文摘要,蒙沈文龙、张文定同志分别代为绘图和摄制照片,在此一并致谢。

一、标 本 描 述

啮齿目 Rodentia Bowdich, 1821

山河狸科 Aplodontidae Trouessart, 1897

半圆齿鼠亚科 Ansomyinae subfam. nov.

亚科定义 颊齿低冠。P^4—M^3 中附尖双尖或脊形,中等凸出于唇侧,但未完全封闭中央谷;外脊由齿尖及齿脊组成,呈半圆提把形,其唇侧在前尖处平坦,于后尖处稍凸起;后小尖单一;无次尖。下颊齿咀嚼面盆状,具发育的附属小脊;M_{1-3} 的下后尖前后收缩或脊形;具一常与中附尖分开的下后附尖脊;无前边尖;下中附尖发育,有一长、时与第II后小脊连接的下中附尖脊;第II后小脊长,近伸达齿凹中部;下内尖位于下次尖之前;下次

小尖显著；下中尖大，很靠唇侧；P_4 下后尖的唇侧未与外脊连接。

归入属 *Ansomys* gen. nov.，中中新世，亚洲；?*Prosciurus* Matthew, 1903 晚渐新世，亚洲；?*Plesispermophilus* Filhol, 1883，早中中新世（MN3），欧洲。

讨论 上述的 ?*Prosciurus* 仅指我国以 *santungensis* Rensberger et Li 所代表的存疑属。欧洲的 *Plesispermophilus* 属显然系一复系类群，其中的 *P. ernii*, *P. macrodon* 和 *P.* ?*argoviensis* 已被伦斯博格（Rensberger, 1983）订正为 *Parallomys*，归入 Allomyinae 亚科。这里的 ?*Plesispermophilus* 系指以 *P.* ? *descedens* 为代表的一分类单元。至于该属的另外两种，*P. angustidens* 和 *P. atavus* 可否归入该亚科，需进一步研究。

半圆齿鼠属（新属）*Ansomys* gen. nov.

属名称由来 前缀 Ansa（拉丁文），意为半圆提把，示该属上颊齿外脊的形状。

属型种 *Ansomys orientalis* gen. et sp. nov.

属的特征 原尖前臂与前齿带连接。下颊齿主尖多少前后向收缩；无前边尖及前边尖脊；下后尖成一低脊；下次尖向后外角扩张，其前唇侧脊未与下中尖脊相接；下中尖及下次小尖强大，呈三角形；下次脊完整；齿座凹具附属小脊。

归入种 *Ansomys shantungensis* Rensberger et Li, 1986

东方半圆齿鼠（新种）*Ansomys orientalis* sp. nov.

（图版 I, II；图 1）

1983: *Prosciurus* sp.，李传夔等，古脊椎动物与古人类，21(4):313—327。

种名称由来 Orientalis（拉丁文）——东方的，意指该种发现于亚洲。

特征 同属的特征。

模式产地 双沟（IVPP 野外编外编号：82028）。

正型标本 一左 $M^{1/2}$（IVPP V8444；图 1）。

归入标本

双沟 64 枚上、下颊齿（$2DP^4$, $6P^4$, $14M^{1/2}$, $8M^3$; $1DP_4$, $3P_4$, $20M_{1/2}$, $10M_3$）（V 8445.1—64）。

松林庄 5 枚上、下颊齿（$1M^{1/2}$, $1P_4$, $3M_{1/2}$）（V8445.65—69）。

郑集 4 枚上、下颊齿（$3M^{1/2}$, $1P_4$）（V8445.70—73）。

时代与层位 中中新世；下草湾组。

描述 颊齿低冠。P^4 次三角形（图版 I，图 1—3）。原尖大，其前、后臂成陡脊，分别伸达牙齿的前缘和后缘。没有次尖。前尖略大于后尖，前者的外侧面平，后者的微凸。中附尖由两个小尖组成，双尖为一高的脊连接；在半数标本上，可见中附尖未完全把中央谷封闭（图版 I，图 1, 2）。前尖及其后脊、后尖及其前脊与中附尖组成一半圆提把形的外脊。原脊完整，向后弯曲，其上的原小尖有一弱的前唇侧脊，在四个标本中，这一脊连结于前边尖的后脊（图版 I,1）。后脊较弱，在五个标本中，这一脊几乎或完全断开（图版 I,2）；后小尖比原小尖大，呈单一的三稜柱状，其后方脊与后齿带连接，前方脊则接于原脊或原小尖；后小尖与原尖为后舌侧窝隔开。前边尖显著，向前突出，时见一后脊。前附尖紧靠前

表 1　测量（单位：毫米）

标本数 N		长度			宽度		
		范围 Range	平均 X	标准差 S	范围 Range	平均 X	标准差 S
DP^4	2	1.65—1.85	1.75	0.10	1.70—1.90	1.80	0.11
P^4	6	1.85—2.25	2.03	0.08	2.05—2.50	2.35	0.08
$M^{1/2}$	19	1.45—1.85	1.59	0.10	2.15—2.60	2.39	0.13
M^3	8	1.35—1.50	1.43	0.05	1.85—2.05	1.90	0.07
DP_4	1	1.50			1.35		
P_4	5	1.60—1.90	1.75	0.10	1.55—1.90	1.77	0.13
$M_{1/2}$	23	1.55—1.90	1.75	0.08	1.50—1.90	1.71	0.11
M_3	10	1.50—1.70	1.60	0.08	1.45—1.60	1.52	0.05

边尖，往唇后侧伸出一达前尖外侧的脊。前边附尖极弱。中央窝壁常有发育的次小脊。四个牙齿的原脊与后脊间尚有一弱脊(图版 I,2)。P^4 三根。

M^1 与 M^2 彼此相似（图版 I, 4—7; 图 1)。与 P^4 的差异在于没有前边尖及前边尖附尖，前附尖极弱，因而牙齿呈长方形；中央谷较宽阔，后脊也稍发育。其个体变异如同 P^4 一样显著：有两个标本的后脊几乎完全断开(图版 I, 4)，约半数标本的中央谷未被封闭(图版 I, 5)；在一些标本中可见中附尖双尖（图版 I, 6)；5 个牙齿的原脊和后脊间皆有一弱脊（图版 I, 7)；多数牙齿都有一中脊的痕迹（图版 I, 5，参见 Schmidt-Kittler and Vianey-Liaud, 1979)；10 个标本前尖的前舌侧有一明显的脊，其中 7 件的这一脊伸达牙齿的前齿带(图版 I, 5)。中央谷中附属次脊的发育程度亦很不一。M^{1-2} 三根。

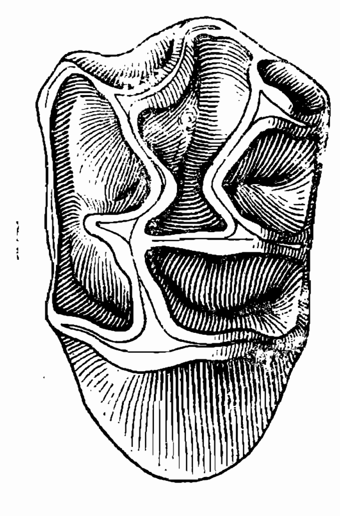


图 1　东方半圆齿鼠(新属、种)，左 $M^{1/2}$，正型标本，V8444，冠面视
Fig. 1　*Ansomys orientalis* gen. et sp. nov. left $M^{1/2}$, type (V8444), occlusal view

M^3 的构造和形态与 M^{1-2} 者很相似（图版 I, 8—10)，不同在于中附尖不甚外凸，后尖较退化，后附尖缺失或极弱，牙齿的后外缘呈弧形，后齿带比前齿带明显短。M^3 尖与脊的变异更为显著；在多数标本中，后小尖不同程度地侧向压扁（图版 I,8)；有三个标本的后小尖没有伸达后齿带的后方脊（图版 I,10)；一个牙齿的后尖与后小尖间缺失后脊(图版 I,8)。M^3 三根。

DP^4 与 P^4 很相似，唯个体较小，前边尖更往前伸，连接齿尖间的脊较为低弱（图版 I, 11—12)。

P_4 呈前窄后宽的梯形。下原尖和下后尖近锥状，不像其它主尖或者臼齿中的尖那样脊形；两齿尖较高、紧靠、彼此为前谷隔开。下后尖最高，比下原尖位置略靠前。下后附尖脊

陡直，与中附尖间总有一凹缺。内下后尖脊在齿凹中分叉，舌侧枝逐渐消失于齿凹的前内侧；唇侧枝较粗壮，常折向舌侧，与下中附尖脊连接。下原尖的前脊向下弯伸，末端在前谷前方略膨大；舌侧脊短，斜向后内侧，在5个牙齿中，有4个的这一脊几乎连接于下后尖的唇后脊(图版 II, 2)。 下中附尖低而较弱小。下中尖及跟座上的其它尖和脊的形状和排列，与 M_{1-2} 者无大异，详见以下描述。 P_4 双根。

M_{1-2} 近方形(图版 II, 3—10)，跟座略宽。下次尖最显著，略向牙齿的后外角扩伸，位于下内尖之后；其唇侧脊向前斜伸，但未与下中尖脊连接，舌侧脊伸达下次小尖。下中尖相当大，呈三角形；唇侧有一把外谷分开的陡脊，在约半数标本中，该脊伸达牙齿的外缘(图版 II, 3)。 下原尖比下次尖略小；其前脊粗壮，前伸并在牙齿的前外角形成一小的结节。下后尖退化成一低脊，在所有的标本中，未见有尖状的下后尖。下后附尖脊低，但完整，末端常膨大成一小尖，小尖常向齿凹伸出一短而弱的小脊；下后附尖脊多以一凹缺与下中附尖分开，仅两件标本有明显的连结趋势(图版 II, 8)。 下中附尖比 P_4 的粗大，位于舌侧缘之中部，呈前后压扁的脊形。下中附尖脊长，或连接于下次脊之中部 (7个标本，见图版 II, 3)，或与第 II 后小脊的后枝连接 (5件标本，II,5)，或同时连接于两者 (8件标本，II, 4)，与第 II 下后脊前枝连接的仅有两标本 (II, 10)；下中附尖与下内尖间有一深的舌侧谷。下内尖比下中附尖大，略小于下原尖，亦呈前后压扁之脊状。下次小尖相当发育，呈三角锥状，位于牙齿后侧之中部；其前方有一发育程度变异大的小脊，在8个牙齿中，该小脊较弱(图版 II, 6)，9件标本中的连接于下次脊(图版 II, 8)。 外脊完整，于下中附尖的前后均弯曲；在10个牙齿中，中附尖前内侧有一指向舌侧的小刺或短脊。 第 II 后小脊从下原尖横向伸出，并常在齿凹中部约靠唇侧的位置上分成两枝，前枝于齿凹前外侧再分成一些细脊，后枝侧连结于下中附尖脊或消失于齿凹中，仅一标本的后枝与下次脊连接 (图版 II, 9)。 下次脊连续，中部略向前弯曲，外端于下中尖中部或稍后处与外脊连结。 单个牙齿难以判别 M_1 或 M_2。较明显的区别可能在于前者的前部相对较窄。 M_{1-2} 四根。

M_3 与 M_{1-2} 的构造相似(图版 II, 11—14)。牙齿附属脊的变异亦同前两臼齿，不同的只是其下次尖相对较大，下内尖和下次小尖较退化，且前者的位置不很靠舌侧，因而使牙齿的后内角呈圆弧形。 M_3 三根。

DP_4 与 P_4 相似，唯个体较小，较为引长，内下后尖脊直、不分叉，下次脊向前凸出并把齿凹分开，后舌侧谷扩大，外谷较开阔(图版 II, 15)。

比较 一般认为，根据牙齿的形态和构造特征，山河狸科可分为四个亚科(见 Rensberger, 1975, 1981, 1983; 王伴月，1987)。 它们是北美晚始新世 (?) 至早中新世及欧洲和亚洲大陆渐新世的 Prosciurinae Wilson, 1949; 北美和亚洲 (?) 晚渐新世至早中新世的 Meniscomyinae Rensberger, 1981; 北美渐新世至早中中新世和欧亚渐新世的 Allomyinae Marsh, 1877, 以及北美晚中新世到现代和亚洲最晚中新世的 Aplodontinae(?) Zittel and Schlosser, 1911。

Prosciurinae 和 Aplodontinae 分别系一类较原始和较特化的山河狸。前者上颊齿中央谷的唇侧完全开放；除一些归入该亚科尚有疑义的属外，都没有外脊；中附尖小，不向唇侧凸出；原脊和后脊较直；下臼齿附属脊不发育；下次脊往往不完整 (Matthew and

Granger, 1923; Wilson, 1949a, b; Galbreath, 1953; Black, 1965, 1971; Kowalski, 1974; Rensberger, 1975)。后者的颊齿很高冠；中附尖极向唇侧凸出；其它附尖及 P^4 前附尖叶完全退化；下臼齿的三角座缩小，而跟座增大 (Rensberger, 1975)。显然，泗洪山河狸与上述两亚科的特征相差甚远。

Meniscomyinae 仅有 *Meniscomys*, *Neglarodon*, *Rudiomys*, *Sewlleladon* 和 *Promeniscomys* 五属 (Rensberger, 1983; Black, 1961; 王伴月, 1987)。泗洪山河狸在后小尖单一，无次尖及下臼齿没有前边尖脊等方面与 Meniscomyinae 各属相似。但其中附尖具双尖；外脊由尖、脊组成，呈半圆提把形，较向外凸出，并未完全把中央谷封闭；下颊齿咀嚼面呈盆状，具发育的附属小脊；有下后附尖脊；下臼齿无锥状的下后尖；下次尖往后唇侧扩伸，并位于下内尖之后；下次小尖很发育；下中尖大且很靠唇侧，P_4 下后尖唇侧脊往后，但不与外脊连接。因此，泗洪山河狸与北美及我国的这一亚科的种类之间的差异也相当明显。

与 Meniscomyinae 相比，泗洪的山河狸在下颊齿的形态上似乎更接近 Allomyinae 者：两者 P_4-M_3 的咀嚼面都呈盆状，具下后附尖脊和一些附属小脊，中附尖弱，下次小尖较发育 (Rensberger, 1983)。但在 Allomyinae 中，上臼齿的中附尖强烈外凸，外脊由齿脊构成，中央谷完全被封闭，具次尖，后小尖双尖；下臼齿的下后尖锥状，下内尖和下次尖位置并排，具前边尖脊，下中尖、下次小尖、下中附尖脊及下次脊都很弱等。两者的差异依然显著。

依上所述，泗洪山河狸所具有的特征，未落入迄今已建亚科的界限。因此，这里把它当作一新的亚科 Ansomyinae。

在我国第三纪中晚期地层发现的山河狸化石，计有 *Promeniscomys*, *Haplomys*, *Prosciurus* 和 *Pseudaplodon* 四属，并被分别归入上述的 4 个亚科 (Schlosser, 1924; Fahlbusch and al., 1983; Rensberger and Li, 1986; 王伴月, 1987)。除 *Prosciurus*? *shantungensis* Rensberger et Li 外，泗洪山河狸很容易区别于上述我国迄今已报道的属种。*P.*? *shantungensis* 的材料仅有一枚 $M_{1/2}$，采自山东某地钻井的岩心，所属层位经重新核准为晚渐新世东营组的最顶部。虽然山东标本在大小上，在具有显著的下中尖及下次小尖，以及在下次尖极向后外扩伸等方面，它都与 *Prosciurus* 相近，但却以下后尖脊状，下中尖及齿脊高度大，唇侧尖及下内尖向前弯曲，下次脊完整，附属小脊发育而有别之。"*P.*?" *shantungensis* 与 *Prosciurus* 的相似特征，只不过是近祖共性(见下)。这些性状，同样存在于祖先类型副鼠的种类中。山东标本在形态及构造上，几乎无异于江苏材料中的 $M_{1/2}$，只是下次尖更向外凸出，下次小尖及下中尖较强壮，齿尖不那么前后压扁，附属小脊较弱。但这并不妨碍把它和泗洪的山河狸当作同一属。

欧洲中西部的化石山河狸仅有两属：*Sciurodon* 和 *Plesispermophilus* (Stehlin et Schaub, 1951; Schmidt-Kitter et Vianey-Liaud, 1979)。后一属包括六种 *P. ernii*, *macrodon*, *angustidens*, *atavus* 及 *P.*? *desedens* 和 *P.*? *argoviensis*。牙齿的形态和构造，似乎表明该属为一复系类群。如上臼齿，在 *P. ernii* 和 *P. macrodon* 中，中附尖为单尖；中央谷封闭，后小尖双尖，具次尖；*P. angustidens* 的中附尖为双尖，中央谷未完全封闭，后小尖单一，亦有次尖；*P.*? *descedens* 虽在中附尖及后小尖的构造上与 *P. angustidens* 相似，但原

尖较弱，又没有次尖。它们之间的明显差异，使伦斯博格有理由把其中的 *P. ernii*, *macrodon* 和 *argoviensis* 订正为一新属——*Parallomys*，并纳入 Allomyinae 亚科。早中中新世（MN3）的 *P.? descedens* 与泗洪山河狸很相似。如两者的中附尖均为双尖型；外脊由尖、脊构成，呈半圆提把状，向外凸出；后小尖单一；没有次尖；下臼齿的齿尖前后压扁，无尖状的下后尖；下次尖的位置在下内尖之后；下中尖及下次小尖发育；都有显著的下中附尖脊；下次尖均发育等。当然，两者仍有所不同，如欧洲标本原尖前臂未连接于前脊，下臼齿具弱的前边尖，下次尖的前唇侧脊与下中尖脊连接。但这些差异至多限于属一级的水平。

二、讨　论

1. 迄今发现的山河狸化石材料，多为破碎的颌骨及单个的牙齿。目前对山河狸类的划分，也只基于牙齿的构造和形态特征。上颊齿的中附尖、外脊、次尖及后小尖，下颊齿的一些尖脊已在亚科的划分中起着重要的作用，但对上述牙齿要素性状的系统发生史，则仍然不很清楚。为了认识各亚科的系统发育关系，拟对牙齿的构造特征，作下性状分析。分析的主要基础是 Prosciurinae 在地史上出现最早，Aplodontinae 最晚。新亚科 Ansomyinae 比另外两亚科出现较晚的这一事实。

(1) Prosciurinae 的上颊齿没有外脊，而 Aplodontinae 的外脊嵴形。在 Meniscomyinae 中，外脊以尖为主，Ansomyinae 则由尖、脊构成。因此，外脊的出现以及嵴形化似为衍生性状。

(2) Prosciurinae 上颊齿的中附尖很小，不向唇侧凸出，这可能是原始的特征。在 Aplodontinae 中，中附尖很发育，且极向外突出。这表明了中附尖在各亚科的发育与外脊的进化趋势很一致。

(3) 山河狸被认为起源于副鼠类（Wood, 1962）。次尖在副鼠类的各属中一般都相当明显。在山河狸中，仅 Allomyinae 具有次尖，其发育被认为系二次进化的结果。

(4) 在 Allomyinae 后小尖的位置上，牙齿具双尖，这一特征该为一衍生性状。

(5) 下后附尖脊在 Prosciurinae 及 Meniscomyinae 中都不发育，该脊从无到有，从弱到强，可能代表一种进化趋向。

(6) 下前边脊存在于 Allomyinae 中，同样可视作是衍生的。

(7) 附属脊在 Ansomyinae 及 Allomyinae 的种类中发育，而 Prosciurinae 及 Meniscomyinae 的齿凹很光滑。牙齿附属脊的缺失，可能为原始的特征。

(8) 下中附尖的增大及下中附尖脊的发育，被视为近裔性状。

(9) 下中尖发育，位置靠外，及下次尖向后外扩伸，虽然只见于 Prosciurinae 及 Ansomyinae，但这些特征亦同样见诸于副鼠类，故应为近祖性状。

(10) Aplodontinae P^4 前附尖叶的退化，下臼齿齿座缩小而跟座扩大，应为一种特化现象。

总的说来，Ansomyinae 的形态与 Prosciurinae 和 Aplodontinae 都有较大的差异，而与 Meniscomyinae 和 Allomyinae 较为相似。因此，在进化上它也就很可能处于两者之

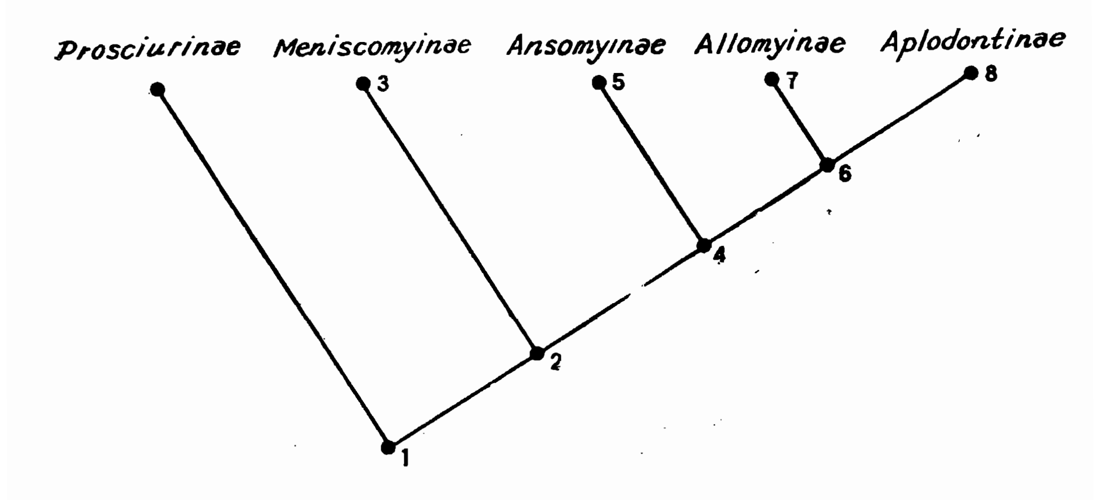


图 2　山河狸各亚科的系统发育关系

Fig. 2　Cladistic hypothesis of aplodontid relationships

间，并与 Allomyinae 和 Aplodontinae 构成山河狸一较高阶元的姐妹分类单元。牙齿性状的系统发育分析，也似乎表明了这点。图 2 为山河狸科各亚科可能的系统发育关系。

节点 1) 代表山河狸科这一单系相对于副鼠类所具有的近裔性状：上臼齿次尖缺失或弱，下臼齿具下中附尖，有较完整的下次脊，下内尖与后边脊分开。

由于 Prosciurinae 的特征原始，又未能确定其近裔自性。因而，它可能代表原始的一枝，并与其它山河狸类构成一姐妹群。

点 2)，除 Prosciurinae 外各亚科共有的近裔性状。这一单系共有着朝上臼齿出现外脊，中附尖向唇侧凸出，下臼齿下中附尖向发育的方向进化。

点 3)，外脊和中附尖的发育似乎向着明显不同的方向独立发展。在 Meniscomyinae 中，外脊以齿尖为主，其中附尖仍处于较原始的状态，但其下臼齿却出现了明显的特化：即由于下次脊及下中附尖脊的加强，使颊齿咀嚼面呈非盆状。这显然是 Meniscomyinae 亚科在山河狸类中的近裔自性。

点 4)，Ansomyinae, Allomyinae 和 Aplodontinae 的近裔共性：上臼齿外脊嵴形，下臼齿具下后附尖脊，以及齿凹中附属小脊发育。这表明在系统发育上较进步的成员在向着使牙齿嵴形化方向发展。

点 5)，Ansomyinae 具有的近裔自性：外脊由尖、脊组成，呈半圆提把状；中附尖双尖；下后尖脊状。

点 6)，Allomyinae 和 Aplodontinae 都更使自己的外脊嵴形化，中附尖更向外侧凸出。

点 7) 和 8) 分别为 Allomyinae 和 Aplodontinae 的近裔自性。前者：二次出现次尖，后小尖双尖；后者：P^4 的前附尖叶退化，下臼齿齿座缩小，跟座扩大。

2. 泗洪山河狸与北美的属种似乎没有很直接的亲缘关系，而与欧洲的一些种类较为亲近。它和“*P.?*” *descedens* 在牙齿构造上的相似，很可能说明它们有一较接近的祖先。

Schmidt-Kittler 和 Vianey-Liaud (1979) 猜想 "*P.?*" *descedens* 系由渐新世的 *P. atavus* 进化而来。确实可能存在这一演化的可能性。除牙齿咀嚼面都为盆状，具有下后附尖外，它们的牙齿还都具有其它种，例如 *P. angustidens* 和 *Sciurodon cadurcensis* 所没有的共同性状：下中附尖及下中附尖脊比较发育，有完整的下次脊，下中尖显著等。其实，只要 *P. atavus* 的下后尖略加压扁，失去其唇后脊，再使下中附尖脊得到发育，即会出现一个 "*P.?*"*descedens* 或 *Ansomys orientalis* 的下臼齿构造型式。因此，*A. descedens* 和 *orientalis* 有一与 *P. atavus* 相似的祖先是可能的。当然，泗洪的 *Ansomys* 是否直接起源于欧洲尚难定论，但可以肯定，目前具有这一新亚科特征的种类，只见于欧亚大陆。

3. 关于下草湾动物群的时代，山河狸标本未能提供确切的证据，但 *Ansomys orientalis* 在形态上与欧洲 Wintershof-West (MN3 带)中的 *A. descedens* 相似，可能说明它们有较接近的进化水平，并代表相近的地质时代。这一情况和推断，与对该动物群松鼠类研究的结论是一致的(见邱铸鼎等，1986)。因此，考虑下草湾动物群的组合，定其时代为中中新世早期，或相当于奥尔良中期 (MN3 顶部—MN5)，从目前看是适宜的。

(1986 年 11 月 4 日收稿)

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THE ARAGONIAN VERTEBRATE FAUNA OF XIACAOWAN, JIANGSU——7. APLODONTIDAE (RODENTIA, MAMMALIA)

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Key words Jiangsu; Miocene; Xiacaowan Formation; Aplodontidae

Summary

The fossils which form the subject of the present study were collected in the recent years from the middle Miocene Xiacaowan Formation at three sites, Songlinzhuang, Shuanggou and Zhengji of Sihong, Jiangsu. Most of the material from the first two sites have been reported previously as *Prosciurus* sp. (Li et al., 1983). Further study indicates that all the specimens mentioned and the $M_{1/2}$ previously assigned to *Prosciurus*? *shantungensis* Rensberger et Li (1986) are quite different from those of *Prosciurus*, but represent a new genus, *Ansomys*. In some features, the new form resembles *Plesispermorphilus*? *descedens* of Europe. For the two taxa a new subfamily Ansomyinae is created. It is morphologically intermediate between Meniscomyinae and Allomyinae, and may be the sister taxon of the higher aplodontids Allomyinae and Aplodontinae.

Family Aplodontidae Trouessart, 1897
Subfamily Ansomyinae (new rank)

Subfamily Definition Cheek teeth brachydont. Mesostyle in P^4-M^3 bifid or lophate, with moderate labial prominence, often not closing labial end of central transverse valley; ectoloph handle shaped and dominated by cusps and crest; labial surface of ectoloph flat on paracone and slightly convex on metacone; single cusp in position of metaconule; hypocone absent. P_4—M_3 basined, with crest extending from metaconid to mesostylid, or separated sometime from mesostylid by a notch; metaconid shortened anteroposteriorly or reduced to a crest on M_1—M_3; anteroconid crest absent; mesostylid developed with long mesostylid crest, sometime joined to metalophulid II; metalophulid II running transversely from protoconid to labial center of basin, absent on metaconid; entoconid placed anterior to hypoconid; hypoconulid pronounced; mesoconid large, very labial in position. P_4 with internal metaconid crest extending posteriad, not toward ectolophid.

Genera *Ansomys* gen. nov., middle Miocene, Asia; ?*Prosciurus* Matthew, 1903, late Oligocene, Asia: ?*Plesispermophilus* Filhol, 1883, middle Miocene (MN3), Europe.

Discussion The genus *Plesispermophilus* of Europe seems to be a polyphyletic group. ?*Plesispermophilus* mentioned here is the taxon represented by *P.* ?*descedens*. Whether the other species, *P. atavus* and *P. angustidens* should be included in a broadly defined Ansomyinae needs further affirmation.

Ansomys gen. nov.

Derivation Nominis Ansa, Latin-handle, a prefix, referring to the handle form ofectoloph.

Diagnosis Anterior arm of protocone connected to anterior cingulum. On lower cheek teeth main cusps more or less compressed anteroposteriórly; metaconid lophate and reduced in height; basal part of hypoconid greatly extended posterolabially; without anteroconid and anteroconid crest; labial crest of hypoconid slanting obliquely forward, but disconnected with mesoconid crest; mesoconid and hypoconulid large and triangular; hypolophid complete; trigonid basin with accessory crests.

Ansomys orientalis sp. nov.

(pl. I-II; fig. 1)

Etymology In allusion to its occurrence in Asia.

Diagnosis As for the genus.

Type Locality Shuanggou.

Type A left $M^{1/2}$ (V 8444).

Measurements See the Chinese text.

Description The cheek teeth are brachydont. P^4 is subtriangular. The protocone is the largest cusp, with a sloped anterior and posterior crest. There is no hypocone. The mesostyle is composed of two cusps connected by a high crest. The cusp is more prominent than that of meniscomyids. The ectoloph is handle-shaped, consisting of paracone, metacone and their anteroposterior arms, plus the parastyle and mesostyle. The labial surface of the ectoloph is flat at the paracone, while it is slightly convex at the metacone. The protoloph is complete and curved backward. The protoconule has a weak anterolabial crest which reaches the posterior crest of the anterocone in four specimens. The metaloph is poorly developed, broken or nearly broken in five teeth. The metaconule is single cusped. It is triangular with a crest extending posteriorly from the apex to join the posterior cingulum, and an anterior crest tending to join the protoconule or the protoloph. The metaconule is separated from the protocone by the posterior lingual fossette. The anterocone is pronounced and projects anteriorly, with variable development of a posterior crest. The parastyle is joined tightly to the anterocone. The anterostyle is essentially a swelling of the anterior cingulum near the anterocone. The labial end of the central fossette is not completely closed by the mesostyle. On the walls of the fossette there are some accessory crests variable in their development. A vestige of mesoloph in two specimens and a weak connection between the protoloph and metaloph in four teeth can be observed. P^4 has three roots.

M^{1-2} are rectangular with a rather wide central fossette. They differ from P^4 in the reduction of a parastylar lobe and the absence of anterocone and anterostyle, and in having a stronger metaloph. They are no less variable than P^4 in minor details: in two specimens the

metaloph is broken; the central fossette is open labially in about half of the teeth; in five specimens the protoloph is connected with the metaloph by a crest; a visible mesoloph exists in most of the specimens; in ten teeth the paracone possesses a striking anterolingual crest, 7 of which extend to the anterior cingulum. The accessory crests in the central fossette are also variable in their development. M^{1-2} are three-rooted.

M^3 is distinguished from M^{1-2} by its mesostyle projecting less labially, metacone more reduced, metastyle absent or poorly developed, and posteroloph shorter than the anteroloph. There is also great variation of the cusps and crests in this tooth. The metaconule is more or less elongated in most of the specimens, it lacks a posterior crest in three teeth. In one tooth the metaloph is absent. M^3 has three roots.

DP^4 is close to P^4 in morphology, but differs from the latter in smaller size, more expanded anterocone, lower and weaker crests.

The lower cheek teeth are basined. P_4 shape is a trapezoid with high and shap protoconid and metaconid. The metaconid is set close to, but separated from, the protoconid by the anterior inflection. The metastylid crest is developed and quite steep. There is a notch between the crest and the mesostylid. The internal metaconid crest is usually bifurcated, with the lingual branch disappearing gradually anterolingual to the center of the trigonid and the labial branch bending to meet the mesostylid crest. The metaconid II is short and extends posterolingually. In 4 out of 6 specimens the crest is connected to the labial branch of metalophid II. The mesostylid is low and relatively weak. The other cusps and crests on the talonid of P_4 resemble those of M_{1-2} described below. P_4 is double-rooted.

M_{1-2} are quadrate with the talonid slightly wider than the trigonid. The hypoconid is a prominent cusp whose position, in occlusal view, is posterior relative to the entoconid. Its labial crest slants forward, but does not connect with the mesoconid. The mesostylid is large and triangular, its labial apex forms a sharp and steeply sloping ridge which reaches the buccal edge in half of the specimens. The anterior crest of the protoconid runs anteriad and forms a very weak tubercle on the anterolabiad corner of the tooth. The metaconid is noncuspate, developed essentially as a thick and low crest. The metastylid crest is complete, terminating usually with a small cuspule. The metastylid crest is often separated from the mesostylid by a notch, only in two specimens does the crest merge with the stylid. The mesostylid is shortened anteroposteriorly. It is relatively more prominent than that of P_4. The cusp is separated from the entoconid by a deep lingual inflection. The mesostylid crest is long and unites with the median part of the hypolophid (7 specimens), with the posterior branch of the metalophid II (5 spec.), or with both of them (8 spec.). It joins the anterior branch of metalophid II only in two teeth. The entoconid is also shortened anteroposteriorly. The hypoconulid is triangular, developed with a crest extending forward from the anterior apex of the cusp. In 9 specimens the hypoconulid crest is connected with the hypolophid. The ectolophid is complete and inflected anterior and posterior to the mesoconid. There is a spur or short crest anterolingual to the mesoconid in 10 specimens. The metalophulid II is directed down the outer surface of the protoconid and divides usually into two braches labial to the center of the trigonid. The anterior branch divides again into several faint crests, while the posterior branch disappears rapidly or joins the mesostylid crest. Only in one tooth, does the posterior branch connect with the hypolophid. The hypolophid is strong and joins the ectolophid at the center or at posterior side of the mesoconid. M_{1-2} has four roots.

M_3 is similar to M_1 and M_2 in occlusal pattern and in variation of the accessory crests, dif-

fering only in the enlargement of the hypolophid and the reduction of the entoconid and hypoconulid. In addition, the less lingually situated entoconid results in having a bow-shaped posterolingual corner in the M_3. The tooth is three-rooted.

DP_4 is similar to P_4, but differs from the latter in being smaller, longer relative to the width, in the interior metaconid crest straight and undivided, the bent hypolophid setting apart the central fossettid, the posterior labial fossettid extended, and in the labial inflection wider.

Comparisions The author follow Rensberger in recognizing the subfamilies Prosciurinae, Meniscomyinae, Allomyinae and Aplodontinae (Rensberger, 1975, 1981, 1983). The Prosciurinae and Aplodontinae show distinctive primitiveness and specialization respectively. In Prosciurinae the mesostyle is small without labial prominence, the ectoloph is absent except in the questionablly referred *Cedromus*, the accessory crests in the valleys or basins are absent or weak, and the hypolophid is incomplete. In the Aplodontinae the teeth are hypsodont with extremely prominent labial mesostyle in the upper cheek teeth, the parastylar lobe of P^4 and the trigonid of lower molars are reduced, while the talonid is enlarged. The teeth from Xiacaowan correspond in some structures to the subfamily definition of Meniscomyinae; such as, single cusp in the position of metaconule, without hypocone and anteroconid crest. Nevertheless, they are beyond the limit of meniscomyines in the following features: mesostyle bifid; ectoloph handle-shaped, dominated by cusps and crests, and incompletely closed labial end of central transverse valley; lower cheek teeth basined with metastylid crest and accessory crests developed; metacone of M_{1-3} lophate. Some characters ol lower molars, for example, the basin shape, the presence of the metastylid crest and mesostylid crest, and the development of the hypoconulid and the accessory crests, are suggestive of the condition in allomyines, but distinguished readily from all the genera of Allomyinae by the lophate metaconid, greater posterolabial extension of the basal part of the hypoconid, absence of the anteroconid crest, possession of more developed mesoconid, hypoconulid, mesostylid and hypolophid. The upper cheek teeth of allomyines are characterized by having their cusps and crests dominating the ectolophs, the prominent labial mesostyle, which is W-shaped and closes the labial end of the central transverse velley, and by the presence of a hypocone and double cusps in the position of the metaconule. Thus, the possibility of the assignment of this material to any defined subfamily of Aplodontidae, except for a new taxon, is excluded by the characteristic structure of the teeth.

Four genera of Aplodontidae, *Promeniscomys, Hypolomys, Prosciurus* and *Pseudaplodon* have been recognized in the Chinese Tertiary deposits and assigned respectively to the four subfamilies (Schlosser, 1924; Rensberger et Li, 1986; Wang, 1987). Among them, the characters of *Prosciurus? shantungensis* Rensberger et Li, such as the lophate metaconid, the great height of the crests, the developed mesoconid, the rather anterior slant of cusps, and the very complete hypolophid, do not fit the diagnosis of *Prosciurus*. *P.? shantungensis,* represented by a $M_{1/2}$ from a well core of Shandong differs from the new form only in having a stronger hypoconule and mesoconid and the less anteroposterior shortened cusps. They are treated here as one genus.

The diverse dental pattern of the European *Plesispermophilus* seems to indicate that the genus is a polyphyletic group. There specie, *P. ernii, P. macrodon* and *P. argoviensis* have been assigned to a new genus *Parallomys* and referred to Allomyinae (Rensberger, 1983). The Miocene taxon, *P.? descedens* and the Xiacaowan aplodontid, seem to share a number of characteristics. These are the bifid mesostyle, the handle-shaped ectoloph dominated by cusps and crests, the single metaconule, the absence cf hypocone, the lophate metaconid, the great posterolabial extension of the hypoconid, the developed mesococonid, hypoconulid and hypolophid, plus the

pronouced mesostylid crest. Although some differences between the two forms can be detected, they still fall into a single subfamily category.

Discussion Based on the paleontological data, character analysis of the main dental features is as follows:

Primitive	Derived
1. Upper cheek teeth without ectoloph.	1. Upper cheek teeth with ectoloph.
2. Mesostyle small without labial prominence.	2. Mesostyle large with great labial prominence.
3. Single cusp in the position of metaconule.	3. Double cusps in the position of metaconule.
4. Metaconid cuspate.	4. Metaconid lophate.
5. Metastylid crest absent on lower molars.	5. Metastylid crest present on lower molars.
6. Anteroconid crest absent on lower molars.	6. Anteroconid crest present on lower molars.
7. Accessory crests absent on the valleys or basins.	7. Accessory crests present on the valleys or basins.
8. Mesostylid small.	8. Mesostylid large.
9. Mesostylid crest weak or absent.	9. Mesostylid crest developed.

It has been speculated that aplodontids might have been derived from paramys-like ancestor. Development and labial arrangement of mesoconid and posterolabial extension of the basal part of the hypoconid in Prosciurinae and Ansomyinae should be of primitive retention (plesiomorphs), but the presence of a hypocone in Allomyines, which appears to be primitive, may be a result of evolutionary reversal. Reduction of the parastylar lobe of P^4 and trigonid of lower molars, and enlargement of talonid is probably a specialization.

From the viewpoint of overall morphological similarity, the new Subfamily Ansomyinae is intermediate between Meniscomyinae and Allomyinae. Thus, Ansomyinae has an ectoloph dominated by cusps and crests, and a moderately prominent labial mesocone. On the one hand, presence of a single metaconule and absence of a hypocone demonstrate that Ansomyinae closely resembles Meniscomyinae; on the other hand, the basin-shaped lower molars, the developed accessory crests and the presence of a metastylid crest show clearly that the new subfamily resembles Allomyinae. Moreover, Ansomyinae lacks features unique to Menisocomyinae and Allomyinae.

A cladistic hypothesis of aplodontid relationships can be corroborated with several dental character-states (see the Chinese text at p. 277).

Node 1. -Monophyly of the Aplodontidae should be corroborated by the possession by all aplodontids of the derived characterstates with respect to other paramyids: hypocone absent or weak; mesostylid and hypolophid present; entoconid separating from posterolophid.

Prosciurinae is the primitive sister-taxon of the other aplodontids because we have been unable to identify autapomorphies of prosciurinae.

Node 2. -The higher aplodontids share the derived characterstates: ectoloph present on upper cheek teeth; mesostyle enlarged and prominent labially; mesostylid crest present.

Node 3. -The straight and cuspidate ectoloph, the developed hypolophid and mesostylid crest of Meniscomyinae are autapomorphies of this taxon within the family.

Node 4. -Ansomyinae, Allomyinae and Aplodontinae have lophate ectoloph along with de-

velopment of metastylid crest and accessory crests. These shared-derived dental features indicate that the three higher subfamilies developed their lophodont crown.

Node. 5. -Autapomorphies of Ansomyinae: ectoloph handle-shaped, dominated by cusps and crests; mesostyle divided; metaconid lophate.

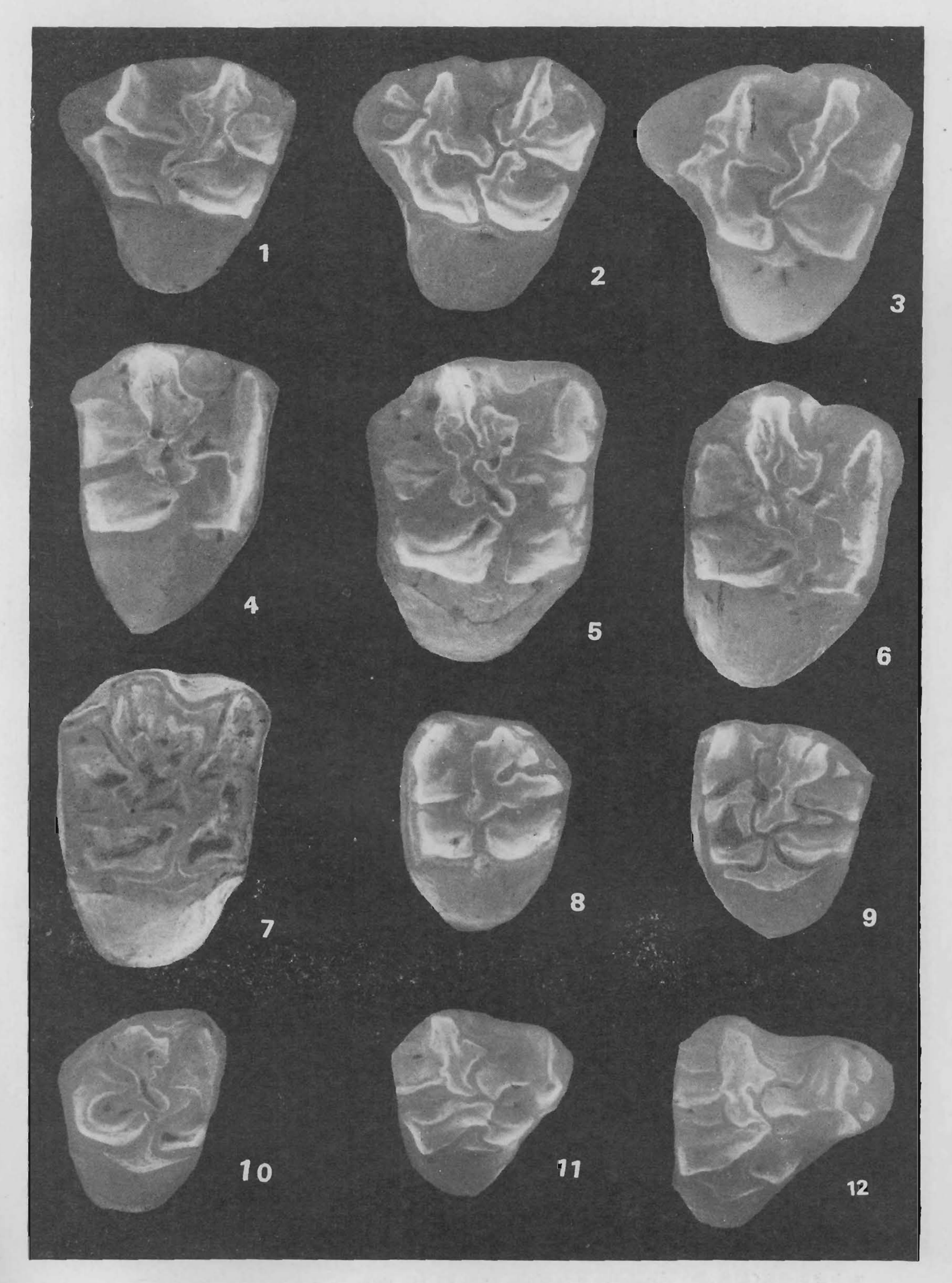
Node 6. -Allomyinae and Aplodontinae possess lophate ectoloph and prominent labial mesostyle. They have more lophodont upper molars than the Ansomyinae.

Node 7. -Autapomorphies of Allomyinae: hypocone present (evolutionary reversal), metaconule divided.

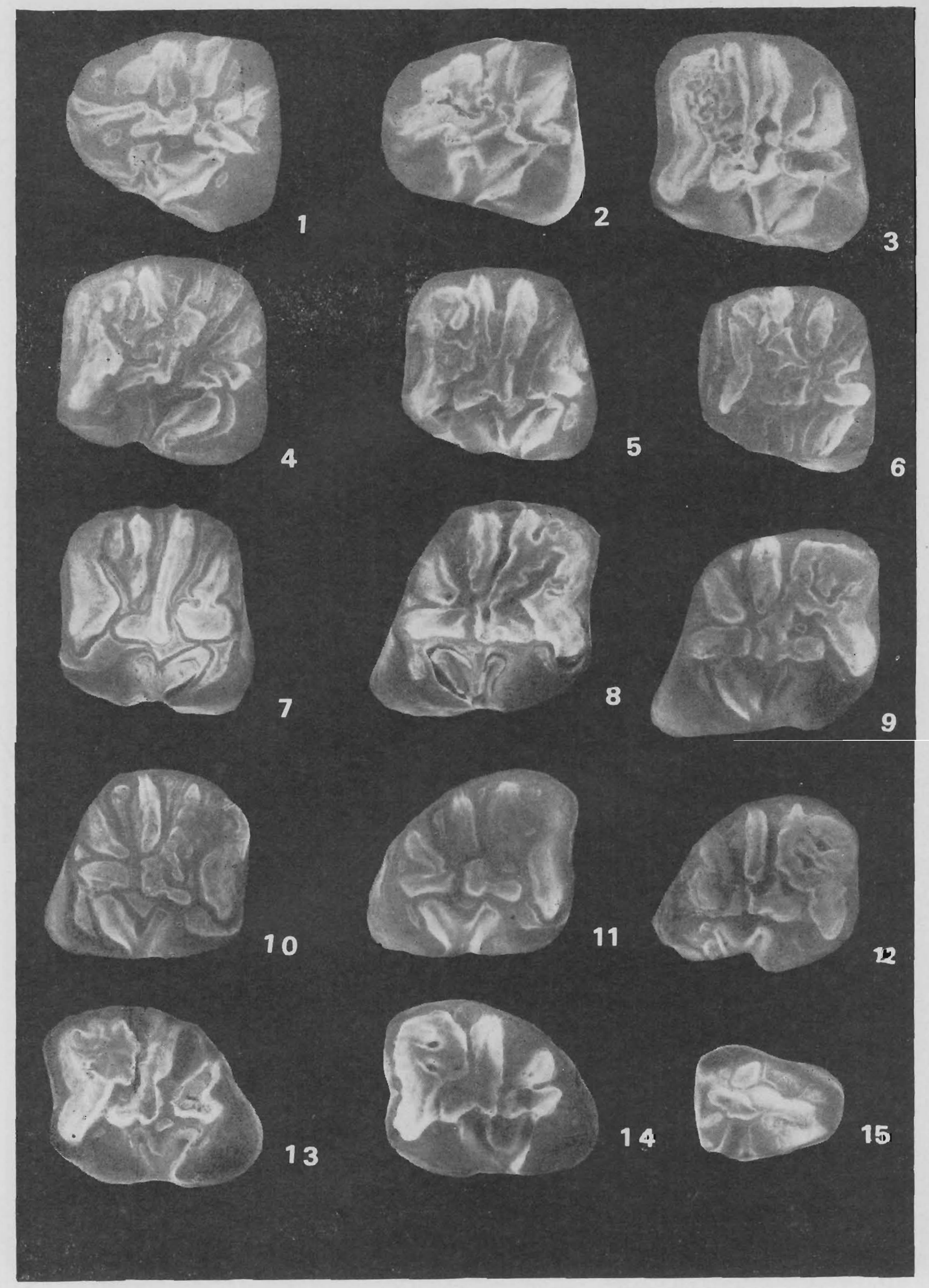
Node 8. -Autapomorphous character-states of Aplodontinae: reduction of parastylar lobe on P^4; trigonid reduced and talonid enlarged on lower molars.

Ansomys seems less closely related to all the known aplodontids of North America, but shares a close relationship with the form like "*P.*"? *descedens* of Europe. The available evidence suggests that *Ansomys* and"*P*"? *descedens* might share a rather close common ancestry. The lower dental structures are suggestive of their derivation from a form like *P. atavus*. The most striking aspects shared are the developed mesostylid and mesostylid crest, and the more developed mesoconid. None of these conditions are shared with other known European species of *Plesispermorphilus* and *Sciurodon*.

Apparently a lower molar of *P. atavus*, if slight shortened anteroposteriorly and better development of the hypolophid would convert into the pattern seen in "*P.*?" *descedens* and *Ansomys orientalis*.



东方半圆齿鼠（新属、种）*Ansomys orientalis* gen. et sp. nov. 1—3. lP^4, V8445.3—5; 4—7. $rM^{1/2}$, V8445. 9—12; 8,9. lM^3, V8445. 23,24; 10. rM^3, V8445. 29; 11, 12. rDP^4, V8445. 1, 2. All ×20



东方半圆齿鼠(新属、种) ***Ansomys orientalis*** **gen. et sp. nov.** 1, 2. lP_4, V8445.32,33; 3—7. $lM_{1/2}$, V8445. 35—39; 8—10. $rM_{1/2}$, V8445.47—49; 11, 12. rM_3, V8445.55,56. 13, 14. lM_3, V8445.59,60; 15. rDP_4, V8445.31. All ×20, except fig. 15 (×15)